

Taxonomic status of the ricefield rat *Rattus argentiventer* (Robinson and Kloss, 1916) (Rodentia) from Thailand, Malaysia and Indonesia based on morphological variation

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Abstract – Comparison of cranial and external characters of 212 ricefield rats *Rattus argentiventer* (Robinson and Kloss 1916), by univariate and multivariate statistical analyses, was carried out on specimens from Thailand, Malaysia, and Indonesia (Sumatra, Kalimantan, Java, Bali, Lesser Sunda, Sulawesi and Irian Jaya). These comparisons indicate that ricefield rats from Thailand to Irian Jaya fall into four groups: a Java group (Thailand, Malaysia, Sumatra and Java); a Bali-Sulawesi group (Bali, Sulawesi, Lombok, Sumbawa, Adonara, Sangeang, Rinca, Flores, Lembata, Alor, Timor and Tanimbar Islands); a Sumba group (Sumba Island) and a Kalimantan group (Kalimantan Island). The specimen from Irian Jaya was placed in the Java group. The taxon from Kalimantan is described as a new subspecies, *R. a. kalimantan*.

The multiple regression analysis indicated that while skull, dentary, dental, and external characters of the ricefield rat do not exhibit sexual dimorphism, age or interactions between islands, sex and /or age does influence some characters.

Key words: Ricefield rat, *Rattus argentiventer*, morphological variation, Thailand, Malaysia, Indonesia.

INTRODUCTION

Recent reappraisal of the mammalian fauna of the Lesser Sunda and Sunda Islands has led to a dramatically different view of the biogeographic boundaries in the Oriental and Australian regions from the traditional ones based on Wallace's and Weber's lines (Kitchener *et al.*, 1990; Kitchener and Maryanto, 1993; Kitchener *et al.*, 1995). The Indonesian archipelago presents unique opportunities to study morphological variation. Comprehensive re-evaluation of morphology in many cases resulted in the discovery of new species and subspecies. In Indonesia such re-evaluation has been conducted, for example, in bats, rodents and primates (Kitchener and Maryanto, 1993; Maryanto *et al.*, 1997; Maryanto and Kitchener, 2000).

The ricefield rat, *Rattus argentiventer*, a rodent species found in ricefields, is often a major pest. It is distributed through Thailand, Vietnam, Cambodia, Laos, Malaysia, Sumatra, Java, Kalimantan, Sulawesi, the Philippines, Lesser Sunda, and has been introduced to New Guinea (van Strien, 1986; Flannery, 1990; Suyanto *et al.*, 1999). There are indications that *R. argentiventer* has different behaviors in different locations (Maryanto, 1991). Recent authors recognized one species (Musser, 1977; van Strein, 1986), however Kitchener and

Suyanto (1996) argued that a detailed examination of morphological variation between island populations is needed to resolve the taxonomic situation of widespread species such as the ricefield rat, especially in the Indo-Australian region.

A number of recent authors have discussed the taxonomic status of the ricefield rat. Prior to Musser's classification of species limits in Asian *Rattus*, most authors treated *R. argentiventer* as a subspecies of *Rattus rattus* (Olerman, 1951; Schwarz and Schwarz, 1967). Musser (1972) initially treated specimens of *R. argentiventer* from Bali, Lombok, Sumbawa, Flores and Timor as a subspecies of *R. rattus*, classifying them as *Rattus rattus bali*. He further considered that *R. r. saturnus* from Sumba Island was synonymous with *R. r. bali*. Specimens from Java were first described as *R. r. brevicaudatus* (Horst and Raadt, 1918) however Chasen (1940) considered this as a synonym of *R. r. argentiventer*. Specimens from Sulawesi described as *R. pestivulus* Thomas, 1921 were referred by Musser (1977) to *R. argentiventer*. Kitchener *et al.* (1990) referred specimens from Lombok to *R. a. bali*.

This paper reports on a taxonomic reappraisal of *R. argentiventer*, as defined above, from Thailand, Malaysia, and Indonesia, based on an examination of morphological variation. Specimens from

mainland Southeast Asia north of the Isthmus of Kra and from the Phillipine islands have not been examined as part of this study.

MATERIALS AND METHODS

A total of 212 adult specimens (see Appendix 1) were studied. The specimens were collected from Thailand, Malaysia, Sumatra, Kalimantan, Java, Sulawesi, Bali, Lombok, Sumbawa, Sangeang, Flores, Adonara, Lembata, Alor, Sumba, Timor, Tanimbar, and from Irian Jaya (Figure 1). All specimens studied are in the collection of Museum Zoologicum Bogoriense (MZB), the Western Australian Museum (WAM) and the Raffles Museum, Zoological Reference Collection, Singapore (ZRC). A specimen was judged to be adult if both the basioccipital/basisphenoid and basisphenoid/presphenoid sutures were fused. Twenty-five measurements of skull, dental and dentary characters and four external characters were measured with calipers to 0.01 mm. The skull characters used were: BB, bulla breadth; BH, bulla height; BL, bulla length; BOZP, breadth of zygomatic plate; BS, braincase breadth; CBL, condillo basal length; GSL, greatest skull length; HB, braincase height; IFB, incisive foramen breadth; IL, incisive foramen length; IO, interorbital breadth; LOD, length of diastema; LOP, length of palatal; M¹W, upper molar 1 width; M¹M¹, upper molar 1 to molar 1; M²M², upper molar 2 to molar 2; M³M³, upper molar 3 to molar 3; MSF, mesopterygoid

fossa width; NB, nasal width; NL, nasal length; DL, dentary length; POW, post orbital width; RAP, ramus angular process; TR, upper tooth row; ZB, zygomatic width. The external characters were HBL, head and body length; TL, tail length; E, ear length and HF, hind foot length. The complete character measurements are shown in Figure 2. The pelage descriptions follow the color terminology of Konerup and Wanscher (1983).

The statistical analyses were run in two steps, univariate analysis and multivariate analysis, as described in Maryanto and Sinaga (1998). Sexes were analyzed separately, as were the skull and external characters. Discriminant Function Analysis (DFA) was initially run for all characters and with all islands as separate groups for island groups. Islands with fewer than four specimens were treated as unallocated island groups. The DFA was then run for a subset of five or more skull characters, based on the criteria of minimized Wilk's lambda to select the best discriminating variables results obtained with the reduced character set were very similar to those based on all characters (Kitchener *et al.* 1993)

RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size are presented in Table 1. These suggest that, except for IFB, MSF,

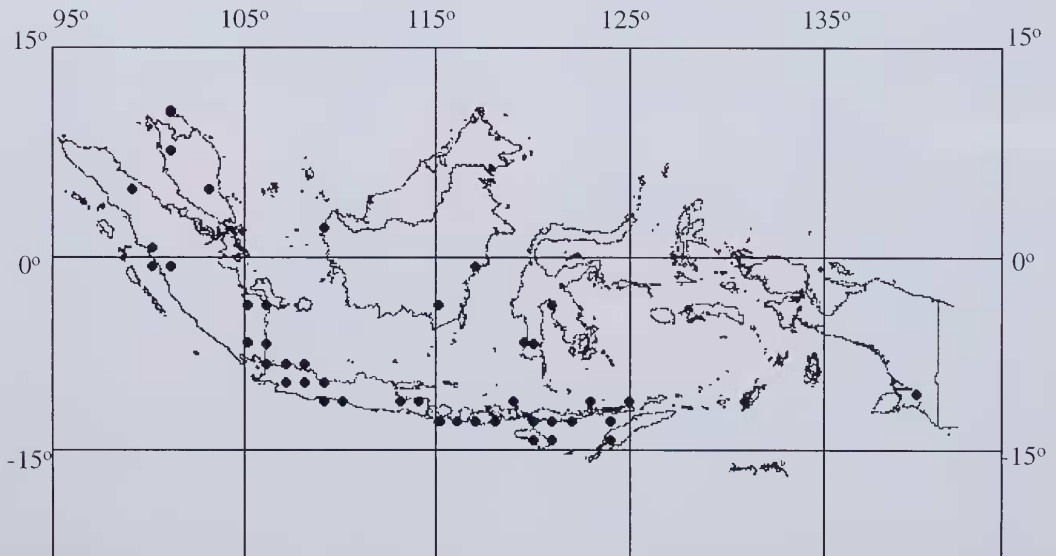


Figure 1 Localities of *Rattus argentiventer* specimens used in this study.

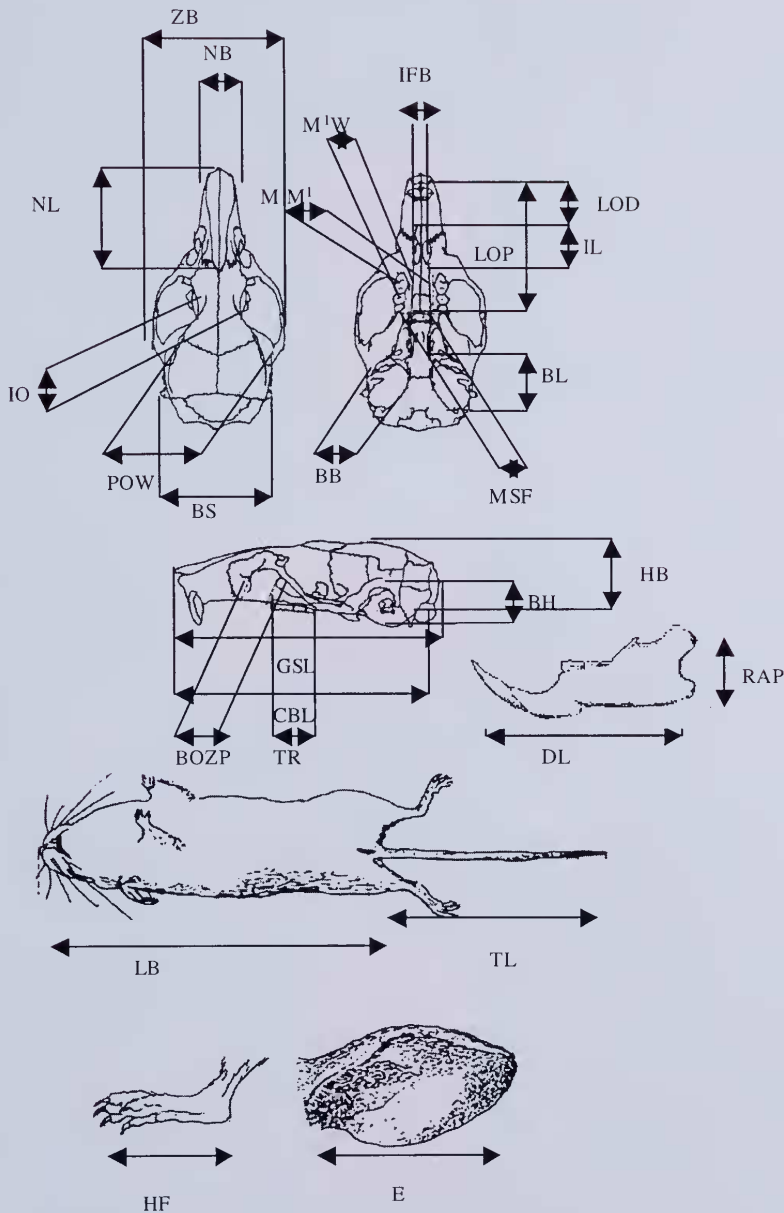


Figure 2 Sketch of the skull, dentary and external character measurements.

M²M² and M³M³, all skull characters in males were slightly larger than in females. Furthermore, the averages of males and females from each group showed that the characters showing sexual differences differed in different groups. For example: The characters in males from Java were slightly larger than in females; nearly all characters in males from the Bali-Sulawesi group were larger than in females, except for IO, MSF, and M¹M¹-

M³M³. Furthermore nearly all characters in males from Sumba were smaller than in females except for GSL, NB, and IFB; and lastly nearly all characters in males from Kalimantan were smaller than in females except for E, HF, MSF, BH, and M¹M¹-

Multiple regression

Multiple regression analysis was employed to

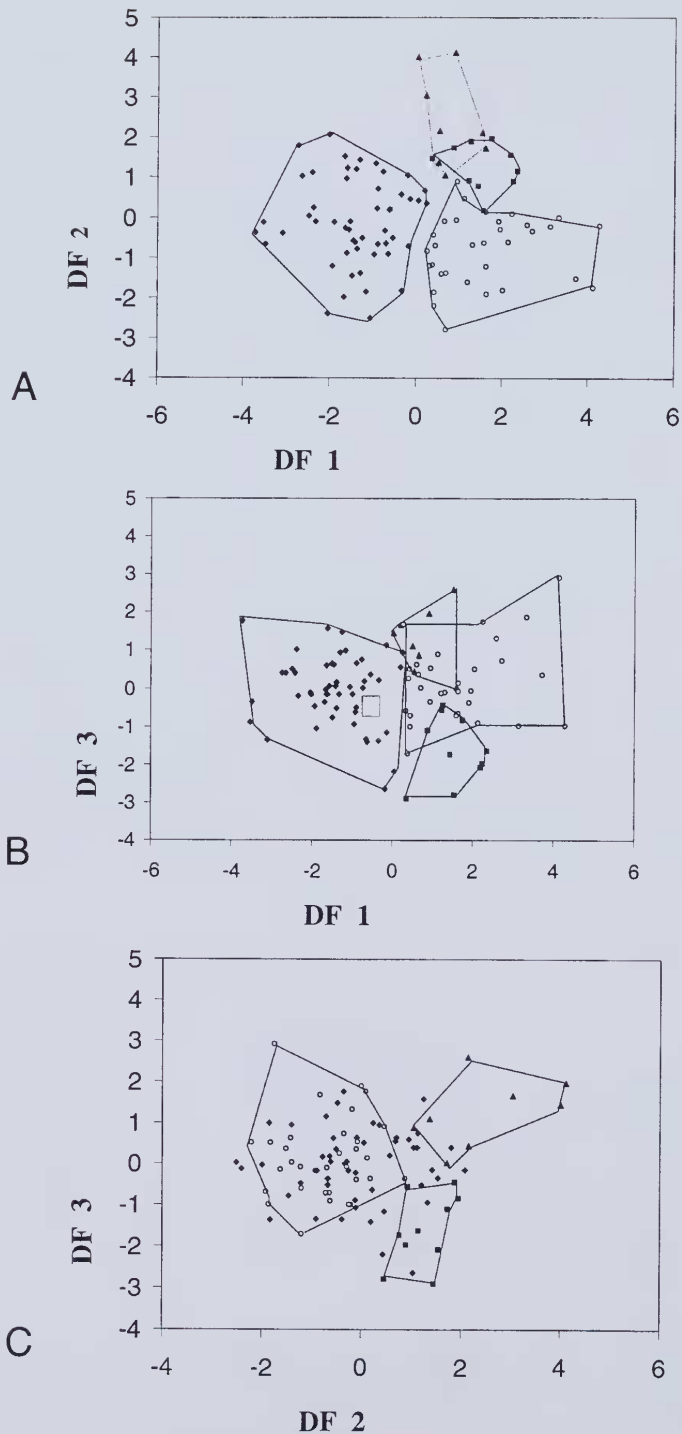


Figure 3 Plot of the female Canonical variate on the following island group populations; \blacklozenge Java group (Thailand, Malaysia, Sumatra, and Java); \blacksquare Kalimantan group (Kalimantan Island); \circ Bali group (Bali, Lombok, Sumbawa, Sangeang, Komodo, Flores, Adonara, Lembata, Alor, Timor and Tanimbar) and \blacktriangle Sumba group (Sumba Island). A. Discriminant Function (DF) 1 vs. Discriminant Function 2 . B. Discriminant Function 1 vs. Discriminant Function 3 and C. Function 2 vs. Function 3.

Table 1 Male and female measurements of the skull, dentary and external characters (in mm).

Group	SEX		LB	TL	E	HF	GSL	ZB	HB	NL	NB	RAP
Java	Male	N	39	43	43	43	52	53	53	52	53	51
		Mean	182.82	168.19	20.05	34.72	41.02	19.74	11.76	14.48	4.41	13.01
		Std. Deviation	16.99	13.13	2.09	2.75	1.66	0.88	0.63	0.99	0.25	0.96
		Minimum	154.00	120.00	16.00	27.00	37.50	17.80	10.80	12.30	4.00	11.30
		Maximum	240.00	192.00	28.00	39.00	44.50	21.40	15.00	16.80	5.20	16.90
	Female	N	39	43	43	43	52	53	53	52	53	53
		Mean	172.38	155.07	19.34	33.33	39.79	19.53	11.59	14.01	4.33	12.67
		Std. Deviation	10.56	15.95	1.68	3.04	1.48	0.74	0.38	0.79	0.30	0.79
		Minimum	147.00	119.00	16.00	29.00	37.20	18.00	10.80	12.30	3.80	11.30
		Maximum	199.00	190.00	23.00	43.00	44.00	21.50	12.40	15.40	5.00	14.90
	Total	N	78	86	86	86	104	106	106	104	106	104
		Mean	177.60	161.63	19.69	34.02	40.40	19.64	11.68	14.24	4.37	12.84
		Std. Deviation	15.00	15.95	1.92	2.96	1.68	0.82	0.53	0.92	0.28	0.89
		Minimum	147.00	119.00	16.00	27.00	37.20	17.80	10.80	12.30	3.80	11.30
		Maximum	240.00	192.00	28.00	43.00	44.50	21.50	15.00	16.80	5.20	16.90
Sumba	Male	N	2	2	2	2	5	6	6	6	6	5
		Mean	152.00	151.50	18.00	32.50	41.76	19.51	11.64	15.03	4.99	12.05
		Std. Deviation	25.46	27.58	1.41	0.00	3.91	1.43	0.37	2.02	0.45	1.13
		Minimum	134.00	132.00	17.00	32.50	37.60	18.20	11.30	12.70	4.70	10.90
		Maximum	170.00	171.00	19.00	32.50	46.70	21.90	12.20	18.40	5.70	13.90
	Female	N	8	7	8	8	9	9	9	9	9	8
		Mean	180.81	168.43	21.06	34.00	41.68	20.39	12.22	15.11	4.83	13.40
		Std. Deviation	20.40	20.39	2.21	1.77	2.80	1.21	0.74	1.32	0.20	1.28
		Minimum	148.00	145.00	17.00	31.00	38.80	18.40	11.00	13.70	4.50	11.60
		Maximum	200.00	191.00	24.00	36.00	47.00	22.00	13.10	17.90	5.10	15.20
	Total	N	10	9	10	10	14	15	15	15	15	13
		Mean	175.05	164.67	20.45	33.70	41.71	20.04	11.99	15.08	4.89	12.88
		Std. Deviation	23.31	21.51	2.39	1.69	3.09	1.33	0.67	1.57	0.32	1.36
		Minimum	134.00	132.00	17.00	31.00	37.60	18.20	11.00	12.70	4.50	10.90
		Maximum	200.00	191.00	24.00	36.00	47.00	22.00	13.10	18.40	5.70	15.20
Bali	Male	N	21	21	20	20	36	35	35	35	36	34
		Mean	175.98	170.60	20.40	34.13	41.44	19.83	11.88	14.93	4.79	13.05
		Std. Deviation	12.57	13.24	1.70	2.17	2.70	1.30	0.69	1.27	0.45	2.07
		Minimum	157.00	144.00	17.00	29.00	36.60	17.10	10.50	12.20	4.00	10.70
		Maximum	213.00	201.00	23.00	37.00	46.50	22.70	13.50	17.50	5.90	22.50
	Female	N	22	22	22	22	37	37	36	37	37	36
		Mean	173.84	161.77	20.80	33.82	40.73	19.76	11.78	14.58	4.68	12.79
		Std. Deviation	14.12	17.51	1.84	2.14	2.27	1.42	0.64	1.00	0.44	2.01
		Minimum	145.00	120.00	17.00	30.50	36.50	17.30	10.50	12.40	4.00	10.50
		Maximum	201.00	194.00	24.00	39.00	45.60	23.20	13.20	16.70	5.60	22.70
	Total	N	43	43	42	42	73	72	71	72	73	70
		Mean	174.88	166.08	20.61	33.96	41.08	19.79	11.83	14.75	4.74	12.92
		Std. Deviation	13.27	16.02	1.76	2.13	2.50	1.35	0.66	1.15	0.44	2.03
		Minimum	145.00	120.00	17.00	29.00	36.50	17.10	10.50	12.20	4.00	10.50
		Maximum	213.00	201.00	24.00	39.00	46.50	23.20	13.50	17.50	5.90	22.70
Kalimantan	Male	N	5	5	5	5	5	5	5	5	5	5
		Mean	167.50	148.10	20.30	35.00	40.17	19.11	11.60	13.86	4.87	12.85
		Std. Deviation	18.43	10.85	0.84	2.83	1.68	1.04	0.35	1.06	0.35	0.86
		Minimum	139.50	135.50	19.00	32.00	38.10	18.20	11.30	12.30	4.60	12.00
		Maximum	187.00	163.00	21.00	38.00	42.50	20.70	12.10	15.10	5.40	14.10
	Female	N	11	11	10	11	12	12	12	12	12	12
		Mean	174.91	156.32	19.50	34.91	40.99	19.90	11.78	14.67	4.90	13.20
		Std. Deviation	14.17	11.09	1.18	2.59	1.52	0.76	0.42	0.76	0.24	0.62
		Minimum	150.00	136.00	17.00	30.00	38.90	18.70	10.80	13.00	4.60	12.30
		Maximum	199.00	172.00	21.00	38.00	44.50	21.00	12.30	15.80	5.20	14.30
	Total	N	16	16	15	16	17	17	17	17	17	17
		Mean	172.59	153.75	19.77	34.94	40.75	19.67	11.73	14.43	4.89	13.09
		Std. Deviation	15.39	11.35	1.12	2.57	1.57	0.89	0.40	0.91	0.27	0.69
		Minimum	139.50	135.50	17.00	30.00	38.10	18.20	10.80	12.30	4.60	12.00
		Maximum	199.00	172.00	21.00	38.00	44.50	21.00	12.30	15.80	5.40	14.30

Table 1 (cont.)

Group	SEX		LB	TL	E	HF	GSL	ZB	HB	NL	NB	RAP
Average – All combined												
Average – All combined	Male	N	67	71	70	70	98	99	99	98	100	95
		Mean	178.61	167.01	20.11	34.51	41.17	19.73	11.79	14.64	4.60	12.97
		Std. Deviation	16.97	14.43	1.92	2.56	2.22	1.08	0.63	1.19	0.41	1.46
		Minimum	134.00	120.00	16.00	27.00	36.60	17.10	10.50	12.20	4.00	10.70
	Maximum	240.00	201.00	28.00	39.00	46.70	22.70	15.00	18.40	5.90	22.50	
	Female	N	80	83	83	84	110	111	110	110	111	109
		Mean	173.98	158.14	19.91	33.73	40.39	19.71	11.72	14.36	4.55	12.82
		Std. Deviation	13.23	16.50	1.85	2.68	1.98	1.07	0.54	0.97	0.40	1.34
		Minimum	145.00	119.00	16.00	29.00	36.50	17.30	10.50	12.30	3.80	10.50
	Maximum	201.00	194.00	24.00	43.00	47.00	23.20	13.20	17.90	5.60	22.70	
	Total	N	147	154	153	154	208	210	209	208	211	204
		Mean	176.09	162.23	20.00	34.08	40.75	19.72	11.75	14.49	4.57	12.89
Std. Deviation		15.18	16.15	1.88	2.65	2.13	1.07	0.58	1.09	0.41	1.40	
Minimum		134.00	119.00	16.00	27.00	36.50	17.10	10.50	12.20	3.80	10.50	
Maximum	240.00	201.00	28.00	43.00	47.00	23.20	15.00	18.40	5.90	22.70		
Group	SEX		DL	M'W	M'L	IO	BOZP	LOP	TR	IL	MSF	IFB
Java	Male	N	52	52	51	53	53	53	53	53	53	53
		Mean	22.80	2.10	3.19	5.71	4.87	19.14	7.00	7.68	2.36	2.59
		Std. Deviation	1.04	0.11	0.22	0.26	0.39	0.92	0.32	0.48	0.22	0.24
		Minimum	20.70	1.90	2.30	5.10	4.00	17.60	5.70	6.60	1.90	2.20
	Maximum	24.60	2.30	3.50	6.40	5.90	21.40	7.50	8.50	2.90	3.20	
	Female	N	53	53	51	53	53	53	53	53	53	53
		Mean	22.47	2.08	3.20	5.55	4.87	18.89	6.87	7.44	2.36	2.55
		Std. Deviation	1.26	0.09	0.20	0.23	0.41	0.89	0.27	0.81	0.20	0.25
		Minimum	20.50	1.90	2.80	5.00	4.00	17.10	6.30	2.80	1.90	2.10
	Maximum	26.00	2.20	3.70	6.00	6.00	21.40	7.40	8.70	2.80	3.30	
	Total	N	105	105	102	106	106	106	106	106	106	106
		Mean	22.63	2.09	3.19	5.63	4.87	19.01	6.94	7.56	2.36	2.57
Std. Deviation		1.16	0.10	0.21	0.26	0.40	0.91	0.30	0.67	0.21	0.25	
Minimum		20.50	1.90	2.30	5.00	4.00	17.10	5.70	2.80	1.90	2.10	
Maximum	26.00	2.30	3.70	6.40	6.00	21.40	7.50	8.70	2.90	3.30		
Sumba	Male	N	6	6	2	6	6	6	6	6	6	6
		Mean	23.11	2.19	3.21	5.70	4.71	19.23	7.07	7.83	2.43	2.60
		Std. Deviation	1.86	0.06	0.08	0.39	0.45	1.48	0.09	0.58	0.14	0.38
		Minimum	21.50	2.10	3.20	5.30	4.30	18.00	7.00	7.40	2.30	2.30
	Maximum	25.80	2.30	3.30	6.40	5.60	21.80	7.20	8.70	2.60	3.20	
	Female	N	9	9	9	9	9	9	9	9	9	9
		Mean	23.78	2.23	3.36	5.79	4.89	20.29	7.37	8.00	2.59	2.52
		Std. Deviation	1.76	0.12	0.22	0.29	0.51	1.43	0.22	0.57	0.20	0.22
		Minimum	21.90	2.00	2.80	5.40	4.40	18.70	7.10	7.30	2.20	2.10
	Maximum	26.20	2.40	3.60	6.20	6.00	22.80	7.80	9.10	2.90	2.90	
	Total	N	15	15	11	15	15	15	15	15	15	15
		Mean	23.51	2.21	3.33	5.75	4.82	19.86	7.25	7.93	2.53	2.55
Std. Deviation		1.77	0.10	0.21	0.32	0.48	1.50	0.23	0.56	0.19	0.29	
Minimum		21.50	2.00	2.80	5.30	4.30	18.00	7.00	7.30	2.20	2.10	
Maximum	26.20	2.40	3.60	6.40	6.00	22.80	7.80	9.10	2.90	3.20		
Bali	Male	N	36	36	23	36	36	34	36	36	35	34
		Mean	22.60	2.14	3.30	6.06	4.78	19.80	7.10	7.85	2.33	2.58
		Std. Deviation	2.32	0.16	0.25	0.29	0.45	1.61	0.38	0.80	0.24	0.26
		Minimum	13.40	1.70	2.80	5.60	3.70	17.00	6.40	6.60	1.90	2.20
	Maximum	27.10	2.40	3.80	6.80	5.70	24.00	7.80	9.70	2.90	3.00	
	Female	N	37	37	20	37	37	37	37	37	37	37
		Mean	22.62	2.13	3.25	6.09	4.64	19.64	7.15	7.41	2.40	2.58
		Std. Deviation	2.37	0.13	0.25	0.40	0.46	1.36	0.37	0.63	0.30	0.28
		Minimum	12.50	1.70	2.80	5.30	3.70	17.60	6.40	6.00	1.90	2.20
	Maximum	26.60	2.40	3.80	6.90	5.70	23.20	8.00	9.50	3.10	3.20	
	Total	N	73	73	43	73	73	71	73	73	72	71
		Mean	22.61	2.14	3.27	6.07	4.71	19.72	7.13	7.63	2.36	2.58
Std. Deviation		2.33	0.14	0.25	0.35	0.46	1.48	0.37	0.74	0.28	0.27	
Minimum		12.50	1.70	2.80	5.30	3.70	17.00	6.40	6.00	1.90	2.20	
Maximum	27.10	2.40	3.80	6.90	5.70	24.00	8.00	9.70	3.10	3.20		

Group	SEX		DL	M ¹ W	M ¹ L	IO	BOZP	LOP	TR	IL	MSF	IFB	
Kalimantan	Male	N	5	5	1	5	5	5	5	5	5	5	
		Mean	22.75	2.20	3.23	5.61	4.61	19.41	6.94	7.45	2.35	2.47	
		Std. Deviation	0.76	0.08	.	0.20	0.33	1.00	0.10	0.45	0.12	0.28	
		Minimum	22.10	2.10	3.20	5.40	4.20	18.30	6.80	6.80	2.30	2.10	
		Maximum	24.00	2.30	3.20	5.80	5.00	21.00	7.00	8.00	2.60	2.90	
	Female	N	12	12	4	12	12	12	12	12	12	12	12
		Mean	23.54	2.19	3.28	5.85	4.90	19.68	7.08	7.48	2.29	2.59	
		Std. Deviation	1.04	0.10	0.12	0.20	0.33	0.75	0.18	0.44	0.25	0.21	
		Minimum	22.10	2.00	3.10	5.60	4.20	18.80	6.80	6.60	2.00	2.20	
		Maximum	25.60	2.30	3.40	6.20	5.40	21.20	7.50	8.00	2.90	3.00	
	Total	N	17	17	5	17	17	17	17	17	17	17	17
		Mean	23.31	2.19	3.27	5.78	4.81	19.60	7.04	7.47	2.31	2.56	
		Std. Deviation	1.02	0.10	0.11	0.22	0.35	0.81	0.17	0.43	0.22	0.23	
		Minimum	22.10	2.00	3.10	5.40	4.20	18.30	6.80	6.60	2.00	2.10	
		Maximum	25.60	2.30	3.40	6.20	5.40	21.20	7.50	8.00	2.90	3.00	
Average – All combined													
Male	N	99	99	77	100	100	98	100	100	99	98	98	
	Mean	22.74	2.12	3.22	5.83	4.82	19.39	7.04	7.74	2.35	2.58		
	Std. Deviation	1.64	0.13	0.23	0.32	0.41	1.26	0.33	0.62	0.22	0.26		
	Minimum	13.40	1.70	2.30	5.10	3.70	17.00	5.70	6.60	1.90	2.10		
	Maximum	27.10	2.40	3.80	6.80	5.90	24.00	7.80	9.70	2.90	3.20		
Female	N	111	111	84	111	111	111	111	111	111	111	111	
	Mean	22.74	2.12	3.23	5.78	4.80	19.34	7.03	7.48	2.38	2.56		
	Std. Deviation	1.77	0.12	0.21	0.38	0.44	1.18	0.33	0.71	0.25	0.25		
	Minimum	12.50	1.70	2.80	5.00	3.70	17.10	6.30	2.80	1.90	2.10		
	Maximum	26.60	2.40	3.80	6.90	6.00	23.20	8.00	9.50	3.10	3.30		
Total	N	210	210	161	211	211	209	211	211	210	209	209	
	Mean	22.74	2.12	3.23	5.80	4.81	19.36	7.03	7.60	2.37	2.57		
	Std. Deviation	1.70	0.13	0.22	0.35	0.43	1.22	0.33	0.68	0.24	0.25		
	Minimum	12.50	1.70	2.30	5.00	3.70	17.00	5.70	2.80	1.90	2.10		
	Maximum	27.10	2.40	3.80	6.90	6.00	24.00	8.00	9.70	3.10	3.30		
Group	SEX		BL	BH	BB	LOD	CBL	M ¹ M ¹	M ² M ²	M ³ M ³	BS	POW	
Java	Male	N	53	53	53	53	51	51	50	50	51	51	
		Mean	7.55	7.07	4.19	11.85	40.24	3.93	4.31	4.74	15.74	16.34	
		Std. Deviation	0.38	0.30	0.33	0.72	2.69	0.35	0.37	0.35	0.57	0.54	
		Minimum	6.50	6.20	3.50	9.90	26.30	3.14	3.50	4.03	14.58	15.27	
		Maximum	8.30	7.60	5.30	13.00	44.60	4.58	5.04	5.62	16.97	17.42	
	Female	N	53	52	53	53	52	53	53	53	53	53	
		Mean	7.38	6.92	4.10	11.52	39.22	3.85	4.17	4.68	15.53	16.26	
		Std. Deviation	0.33	0.24	0.27	0.56	1.45	0.42	0.41	0.39	0.61	0.62	
		Minimum	6.80	6.40	3.60	9.90	36.80	2.98	3.41	3.97	13.71	14.89	
		Maximum	8.10	7.40	4.80	12.80	43.00	4.78	5.34	5.73	16.89	17.92	
	Total	N	106	105	106	106	103	104	103	103	104	104	
		Mean	7.46	6.99	4.15	11.68	39.72	3.89	4.24	4.71	15.64	16.30	
		Std. Deviation	0.36	0.28	0.30	0.66	2.21	0.39	0.39	0.37	0.60	0.58	
		Minimum	6.50	6.20	3.50	9.90	26.30	2.98	3.41	3.97	13.71	14.89	
		Maximum	8.30	7.60	5.30	13.00	44.60	4.78	5.34	5.73	16.97	17.92	
Sumba	Male	N	6	6	6	6	6	6	6	6	6	6	
		Mean	7.71	7.21	4.41	11.79	41.07	3.61	3.93	4.35	16.14	16.33	
		Std. Deviation	0.52	0.39	0.49	1.17	3.67	0.45	0.52	0.51	0.86	0.39	
		Minimum	7.00	6.80	3.90	11.10	36.90	3.01	3.24	3.75	14.91	15.81	
		Maximum	8.60	7.90	5.20	14.20	46.60	4.05	4.54	4.89	17.19	16.90	
	Female	N	9	9	9	9	9	9	8	8	9	9	
		Mean	8.08	7.48	4.48	12.65	41.42	4.02	4.44	4.86	16.52	16.79	
		Std. Deviation	0.68	0.41	0.21	1.00	3.30	0.49	0.59	0.57	0.83	0.63	
		Minimum	7.30	6.90	4.00	11.50	37.70	3.27	3.39	3.83	15.53	15.98	
		Maximum	9.00	8.00	4.80	14.10	47.50	4.68	5.24	5.56	18.18	17.71	
	Total	N	15	15	15	15	15	15	14	14	15	15	
		Mean	7.93	7.37	4.45	12.31	41.28	3.86	4.22	4.64	16.37	16.61	
		Std. Deviation	0.63	0.41	0.34	1.12	3.33	0.50	0.60	0.59	0.83	0.58	
		Minimum	7.00	6.80	3.90	11.10	36.90	3.01	3.24	3.75	14.91	15.81	
		Maximum	9.00	8.00	5.20	14.20	47.50	4.68	5.24	5.56	18.18	17.71	

Table 1 (cont.)

Group	SEX		BL	BH	BB	LOD	CBL	M ¹ M ¹	M ² M ²	M ³ M ³	BS	POW
Bali	Male	N	35	35	35	36	34	29	29	29	31	31
		Mean	7.49	7.00	4.19	12.14	40.67	3.92	4.29	4.73	15.98	16.67
		Std. Deviation	0.39	0.36	0.28	1.23	3.39	0.45	0.46	0.57	0.69	0.67
		Minimum	6.70	6.10	3.70	10.10	28.10	3.06	3.53	3.82	14.53	15.36
		Maximum	8.40	7.60	4.70	15.40	46.10	4.70	5.20	5.64	17.21	18.90
	Female	N	37	37	37	37	37	35	35	35	35	34
		Mean	7.43	6.95	4.14	11.80	40.13	3.97	4.47	4.97	15.70	16.52
		Std. Deviation	0.43	0.33	0.26	1.05	2.42	0.53	0.60	0.58	0.84	0.59
		Minimum	6.40	6.10	3.70	9.50	35.60	3.10	3.39	4.11	14.09	15.44
		Maximum	8.30	7.60	4.60	15.00	45.30	5.01	5.85	6.15	17.32	17.67
	Total	N	72	72	72	73	71	64	64	64	66	65
		Mean	7.46	6.97	4.17	11.97	40.39	3.95	4.39	4.86	15.83	16.59
		Std. Deviation	0.41	0.34	0.27	1.15	2.92	0.49	0.54	0.58	0.78	0.63
		Minimum	6.40	6.10	3.70	9.50	28.10	3.06	3.39	3.82	14.09	15.36
		Maximum	8.40	7.60	4.70	15.40	46.10	5.01	5.85	6.15	17.32	18.90
	Kalimantan	Male	N	5	5	5	5	5	5	5	5	5
Mean			7.57	7.02	4.27	11.64	39.39	3.97	4.22	4.73	16.34	15.92
Std. Deviation			0.32	0.25	0.40	0.45	1.82	0.22	0.19	0.23	0.61	0.38
Minimum			7.10	6.60	3.90	11.10	37.10	3.74	3.89	4.36	15.40	15.51
Maximum			7.90	7.20	4.90	12.10	42.00	4.25	4.34	4.95	17.10	16.54
Female		N	12	12	12	12	12	12	12	12	12	12
		Mean	7.57	7.01	4.34	11.89	40.41	3.99	4.30	4.74	16.34	16.12
		Std. Deviation	0.28	0.21	0.36	0.45	1.49	0.23	0.34	0.43	0.78	0.44
		Minimum	7.30	6.70	3.60	11.40	38.70	3.59	3.66	4.17	14.85	14.97
		Maximum	8.20	7.30	4.70	13.00	43.60	4.38	4.88	5.42	17.39	16.68
Total		N	17	17	17	17	17	17	17	17	17	17
		Mean	7.57	7.01	4.32	11.82	40.11	3.98	4.27	4.74	16.34	16.06
		Std. Deviation	0.28	0.21	0.36	0.46	1.61	0.22	0.30	0.37	0.72	0.42
		Minimum	7.10	6.60	3.60	11.10	37.10	3.59	3.66	4.17	14.85	14.97
		Maximum	8.20	7.30	4.90	13.00	43.60	4.38	4.88	5.42	17.39	16.68
Average - All combined												
	Male	N	99	99	99	100	96	91	90	90	93	93
		Mean	7.54	7.05	4.21	11.94	40.40	3.91	4.27	4.71	15.88	16.43
		Std. Deviation	0.39	0.33	0.33	0.96	2.96	0.39	0.41	0.44	0.65	0.60
		Minimum	6.50	6.10	3.50	9.90	26.30	3.01	3.24	3.75	14.53	15.27
		Maximum	8.60	7.90	5.30	15.40	46.60	4.70	5.20	5.64	17.21	18.90
	Female	N	111	110	111	111	110	109	108	108	109	108
		Mean	7.47	6.98	4.17	11.74	39.83	3.91	4.30	4.79	15.76	16.37
		Std. Deviation	0.44	0.32	0.29	0.84	2.10	0.44	0.50	0.49	0.79	0.62
		Minimum	6.40	6.10	3.60	9.50	35.60	2.98	3.39	3.83	13.71	14.89
		Maximum	9.00	8.00	4.80	15.00	47.50	5.01	5.85	6.15	18.18	17.92
Total	N	210	209	210	211	206	200	198	198	202	201	
	Mean	7.50	7.02	4.19	11.84	40.10	3.91	4.29	4.76	15.81	16.40	
	Std. Deviation	0.41	0.32	0.31	0.90	2.55	0.42	0.46	0.47	0.73	0.61	
	Minimum	6.40	6.10	3.50	9.50	26.30	2.98	3.24	3.75	13.71	14.89	
	Maximum	9.00	8.00	5.30	15.40	47.50	5.01	5.85	6.15	18.18	18.90	

determine the influences of sex, age, localities and the interactions between these factors. All localities were included in the analysis (Malaysia, Sumatra, Java, Kalimantan, Sulawesi, Bali, Lombok, Sumbawa, Sangeang, Flores, Sumba, Adonara, Lembata, Alor, Timor, Tanimbar and Irian Jaya). The results are presented in Table 2.

Sex

Sex by itself had no significant effect at $P < 0.05$ on any individual character.

Age

Most variables showed a significant influence of individual age; exceptions were NB, TR, IL, MSF, BB, RAP, M¹W and M¹L ($P < 0.05$).

Locality

A locality is generally an island, except that the mainland Southeast Asian population is treated as a single locality (Malaysia). The variables ZB, NB, IO, IFB, BH, M¹W, BS, LB, and TL, were significantly influenced by locality.

Table 2 Multiple regressions on sex, age, locality, and the interactions among these factors for *Rattus argentiventer* in skull, dentary and external characters. F values are presented for the main effects and interactions (2 way and 3 way). Significance levels are *) 0.05>p>0.01, **) 0.01>p>0.001 and ***) P<0.001. For explanation of character codes see Materials and Methods.

Dependent Variable	Locality	Sex	Age	Locality Vs Age	Locality Vs Sex	Age Vs Sex	3 way Interactions
LB	3.530*	1.798	7.911***	2.806*	3.080*	3.190*	0.119
TL	4.494**	0.078	5.403**	1.323	0.989	1.950	0.279
E	1.486	0.298	7.077***	2.403	1.216	0.839	0.079
HF	0.836	0.022	0.791	0.070	0.267	0.281	0.143
GSL	1.681	1.846	23.601***	1.798	0.450	1.326	1.771
ZB	3.029*	1.421	16.225***	3.047*	2.278	1.802	0.008
HB	2.308	0.935	8.773***	1.606	0.930	2.938	0.121
NL	1.231	0.162	18.706***	1.082	1.114	0.932	1.184
NB	4.542**	1.574	2.476	0.393	0.707	0.012	0.963
IO	15.608***	1.045	6.579**	0.803	2.731*	0.807	0.008
BOZP	1.421	0.150	5.526**	0.422	0.569	0.410	0.058
LOP	0.126	3.213	14.552***	2.138	3.840*	0.743	0.554
TR	2.496	0.094	0.074	0.312	0.277	0.646	0.915
IL	1.082	2.642	2.316	1.022	0.198	1.512	0.389
MSF	2.679	0.021	2.914	0.658	0.659	0.320	1.251
IFB	3.252*	0.113	6.514**	0.175	2.855*	0.926	1.274
BL	2.330	0.040	8.130***	1.763	0.862	0.158	2.198
BH	3.566*	2.856	4.190*	0.383	1.332	0.676	0.630
BB	1.765	1.317	1.732	1.152	0.171	0.480	1.200
LOD	0.335	0.784	14.566***	1.942	2.991*	0.033	0.728
RAP	0.392	1.141	2.550	3.719**	0.895	1.142	0.265
DL	2.126	0.003	9.316***	1.656	0.382	0.219	1.337
M ¹ W	2.804*	0.006	0.122	0.244	0.459	2.402	0.286
M ¹ L	0.806	0.063	0.355	0.383	0.538	0.477	1.092
CBL	2.421	0.925	27.527***	2.877*	0.619	1.545	1.539
M ³ M ¹	0.562	0.231	10.771***	0.980	0.446	0.272	0.346
M ³ M ²	1.380	0.224	11.644***	2.231	1.494	0.382	0.209
M ³ M ³	2.605	2.571	9.670***	2.664*	2.418	0.286	0.925
BS	3.395*	1.449	7.235***	0.715	0.108	1.018	1.628
POW	2.011	0.806	6.465**	0.851	1.569	0.731	0.036

Interaction

The variables ZB, CBL, M³M³, LB at P<0.05 and RAP at P>0.01 were significantly influenced by the interaction between locality and age. The characters IO, LOP, IFB, LOD and LB (P<0.05) were significantly influenced by the interaction between locality and sex. Except for head and body length (P<0.05) there was no significant influence between age and sex (P>0.05). No variable showed a significant interaction between all three factors.

Multivariate analysis

The regression analysis showed that age strongly influenced many of the skull, dental and dentary characters, either individually or through interactions with sex or locality. Consequently the multivariate analysis was based on fully adult specimens as judged from basicranial fusion.

Although there is little interaction between sexual dimorphism in *R. argentiventer*, a total of five characters (LB, IO, LOP, IFB and LOD) showed a significant difference between sex and locality. For this reason, discriminant function (canonical variate) analysis was performed separately for males and females.

Females

An initial DFA was run using skull, dental and dentary characters and all locations. Because the number of characters employed in this analysis exceeded the sample size of the smallest group (Sumba, N=9), the DFA was repeated using a reduced set of seven characters in order to avoid over fitting the data (Kitchener and Maryanto 1995). The seven characters were selected by minimizing Wilk's lambda on the first canonical variate. The DFA plot was based on seven characters similar to that based on the complete character set. The seven characters in the DFA were IO, BH, BOZP, BS, M³M³, NB and MSF. This analysis extracted three significant functions, which together accounted for 100% of the variation. Discriminant Functions (DF) 1, 2, and 3 accounted for 63.02%, 24.60%, and 12.38% of the variation between populations respectively (Table 3). Each of the functions was highly significant DF1 ($X^2=200.411$; $df=21$; $P=0.00001$), DF 2 ($X^2=91.305$; $df=12$; $P=0.00001$) and DF 3 ($X^2=33.432$; $df=5$; $P=0.00001$). Reclassification of cases resulted in a correct allocation of 95.3% to localities

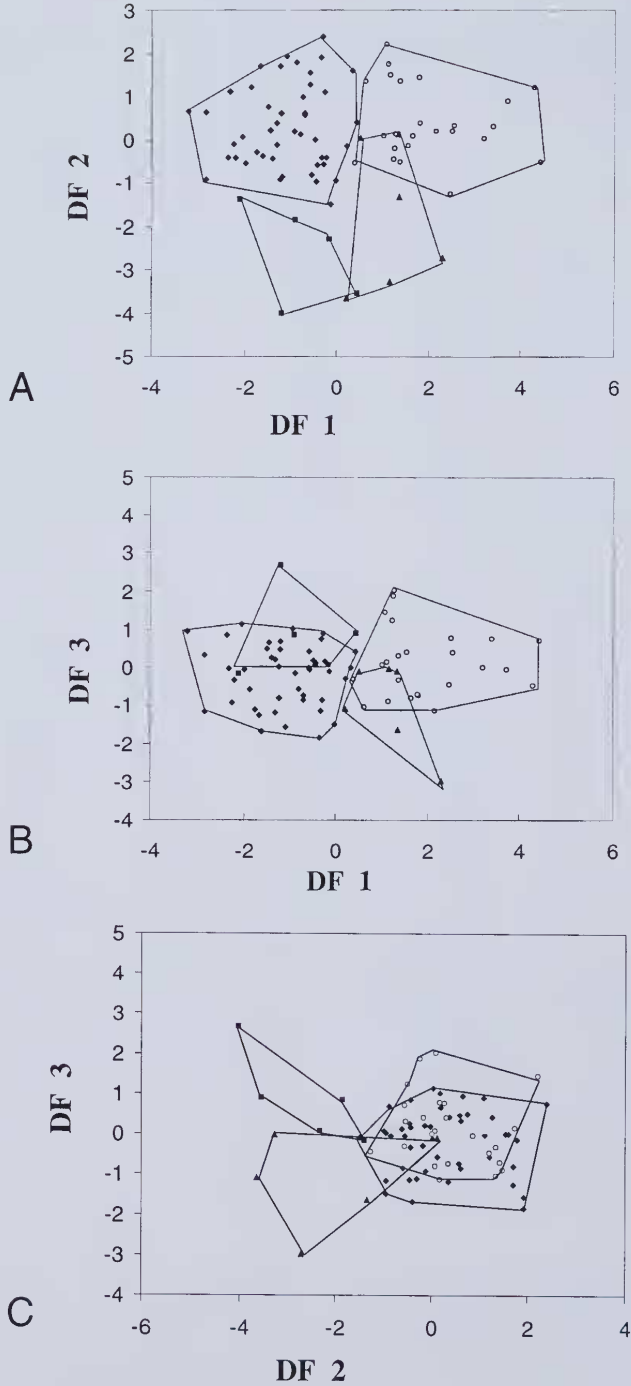


Figure 4 Plot of the male canonical variate on the following island group population 1; ◆ Java group (Thailand, Malaya, Sumatra, and Java); ■ Kalimantan group (Kalimantan Island); ○ Bali group (Bali, Lombok, Sumbawa, Sangeang, Komodo, Flores, Adonara, Lembata, Alor, Timor and Tanimbar) and ▴ Sumba group (Sumba Island). A. Discriminant Function (DF)1 vs. Discriminant Function 2. B. Discriminant Function 1 vs. Discriminant Function 3 and C. Discriminant Function 2 vs. Discriminant Function 3.

Three of the seven characters (BOZP, IO and NB) loaded heavily on DF1 (>0.5). These are evidently major characters, which display regional heterogeneity in populations of *R. argentiventer* in Indonesia. The DFA coefficients from this analysis are given in Table 3.

The configuration of DFA plots suggest that the ricefield rat contains four major morphological subpopulations (Figure 3). These are 1, a Java group (Thailand-Malaysia-Sumatra and Java); 2, Kalimantan; 3, a Bali-Sulawesi group (Bali, Lombok, Sumbawa, Sangeang, Komodo, Flores, Adonara, Lembata, Alor, Timor, Tanimbar and Sulawesi) and 4, Sumba. A bivariate plot between DF1 and DF2 shows that the Java group is separated from the Kalimantan, Bali-Sulawesi and Sumba groups on DF1 (Figure 3). A plot of DF2 against DF3 shows good separation of each of the Kalimantan, Sumba and Bali-Sulawesi groups. A single specimen from Irian Jaya, which was unallocated in the DFA falls within the Java group (Group 1). The Sulawesi population falls within group 3. A total of 94.2% of individuals in the Java group were correctly reclassified, with 5.7% (3 individuals) misclassified as Kalimantan. In the Bali-Sulawesi group, 94.3% of individuals were correctly reclassified with 2 individuals (2.9%) misclassified, one to each of the Java and Kalimantan groups. Finally, 100% (9 specimens and 10 specimens) of individuals from each of Sumba and Kalimantan were correctly reclassified.

Table 3 Standardized and unstandardized (in brackets) canonical variate function coefficients the derived from seven character analysis of female *Rattus argentiventer*

Variable	Function 1	Function 2	Function 3
IO	0.888 (3.784)	-0.472 (-2.014)	0.178 (0.760)
BH	0.066 (0.252)	0.547 (2.087)	0.782 (2.986)
BOZP	-0.794 (-1.953)	-0.218 (-0.537)	-0.289 (-0.712)
NB	0.639 (1.991)	0.437 (1.359)	-0.503 (-1.564)
M ³ M ³	-0.306 (-0.702)	-0.781 (-1.791)	0.420 (0.963)
BS	0.389 (0.589)	0.870 (1.316)	-0.471 (-0.712)
MSF	-0.353 (-1.617)	0.133 (0.609)	0.675 (3.089)
Variation explained	63.02%	24.60%	12.38%
Constant	-25.078	-20.127	-15.232

Males

A DFA for males was run initially for the full set of 24 skull and dentary characters for all islands. However, because the sample size of the smallest groups (Kalimantan and Sumba) was 5 and 6, the analysis was repeated using a reduced set of five characters (BS, IO, NB, NL and M³M³) selected as for the female analysis.

The five characters selected by minimizing Wilk's lambda on the first canonical variate were IO, NB, M³M³, BS, and NL. Three of those variables were

the same as those selected in the female analysis (IO, NL, BS); the others relate to similar components of the skull, namely the rostrum and the palate. The DFA plots produced with the reduced character set are similar to those based on the complete set of characters. This analysis extracted three significant functions, which together explained 100% of the variation. The DF 1: 67.93%, DF 2: 27.48%, and DF 3: 4.59% of each of these functions is highly significant (DF1: $X^2=138.065$; $df=15$; $P=0.00001$, DF 2: $X^2=54.464$; $df=8$; $P=0.00001$ and DF 3 $X^2=9.553$; $df=3$; $P=0.022$). The characters which loaded most heavily (>0.5) on DF1 were IO, M³M³ and NB.

The percentage of individuals correctly reclassified was 87.95%. In the Java group 91.5% of individuals were correctly reclassified with only 4.3% (2 individuals) misclassified to the Sumba group, and 4.3% to the Bali-Sulawesi group. A total of 66.7% of the individuals from Sumba were correctly reclassified with 33.3% (2 individuals) misclassified to the Bali-Sulawesi group. In the Bali-Sulawesi group, 88% of specimens were correctly reclassified with 4% (1 individual) and 8% (2 individuals) misclassified to the Java and Sumba groups respectively. Finally, 80% of individuals from Kalimantan were correctly reclassified with one individual misclassified to the Java group.

The Scatter plot between coefficient canonical 1 and 2 showed that the Java group was separated from the Sumba and Kalimantan groups (Figure 4). This bivariate plot also indicated that the Kalimantan individuals were separate from those in the Java, Bali-Sulawesi, and Sumba groups. Furthermore, individuals from Sumba were not clearly separated from those in the Bali-Sulawesi group.

SYSTEMATICS

Rattus argentiventer argentiventer Robinson and Kloss, 1916

Rattus rattus braivicaudatus Horst and Raadt, 1918

Rattus rattus chaseni Sody, 1941

Holotype

British Museum (Natural History) 19.11.5.89

Type locality

Pasir Ganting, west coast of Sumatra

Diagnosis

Robinson and Kloss (1918:55) described *R. a. argentiventer* as dorsally coarsely streaked, blackish and warm buff, grayer on the sides and limbs. The under parts are not clearly margined and are clad with fur having gray bases and white tips producing a general silvery effect, except on the

throat, which is white. A scarcely indicated buffy median stripe is present on the chest. The feet are parti-colored: tail brown throughout. This description serves equally for specimens from Thailand to Java. The skull of the typical form is distinguished from that of the other subspecies by the combination of a narrower interorbital region and narrower rostrum (Figure 5c).

Distribution

Thailand, Malaysia, Sumatra, and Java, possibly extending to Vietnam, Cambodia, Laos.

Rattus argentiventer kalimantanensis subsp. nov.

Holotype

Museum Zoologicum Bogoriense, MZB22419, adult male, weight 189 grams, carcass fixed in 70% ethanol, skull separated from body, collected by Ibnu Maryanto and M.H. Sinaga in March 2000.

Table 4 Male standard and unstandardized (in brackets) canonical variate function coefficients derived from the five character analysis of male *Rattus argentiventer*.

Variable	Function 1	Function 2	Function 3
BS	-0.309 (-0.524)	-0.781 (-1.318)	0.458 (0.774)
IO	0.848 (3.782)	0.742 (3.308)	0.289 (1.292)
NB	0.675 (2.198)	-0.948 (-3.086)	-0.029 (-0.097)
NL	0.339 (0.347)	0.731 (0.750)	-0.992 (-1.018)
M ¹ M ¹	-0.680 (-2.100)	0.348 (1.075)	0.535 (1.650)
Variation explained	67.93%,	27.48%,	4.59%
Constant	-20.355	0.947	-10.794

Paratypes

See appendix for list of specimens examined

Type locality

Saka Gunung, Sei Kambat, Cerbon, Barito Kuala, South Kalimantan.

Diagnosis

Rattus argentiventer kalimantanensis females differ from *R. a. argentiventer* in averaging slightly larger in all skull dimensions except for BOZP. They differ from individuals in the Bali-Sulawesi group (*R. a. pestivulus*) in averaging slightly larger except dimensions for TR, DL, MSF, M²M², M³M³, POW, IO, TL and E. They differ from individuals in the Sumba group (*R. a. saturnus*) by averaging slightly smaller except for NB, IO, BOZP, LOP, M¹W, IFB, and HF.

Rattus argentiventer kalimantanensis males differ from *R. a. argentiventer* in averaging slightly smaller except for NB, LOP, M¹M¹, POW, BB, M¹W, BL, E, and HF. They differ from *R. a. saturnus* in averaging smaller except for RAP, M¹W, M¹M¹, M²M², M³M³,

BS, POW, LOP, GSL, LB, E, and HF. They differ from *R. a. pestivulus* in averaging slightly smaller except for NB, IO, M¹M¹, BS, BB, PL, M¹W, MSF, BL, BH, and HF.

Scatter plots of skull characters show that the interorbital breadth of male *R. a. kalimantanensis* is generally narrower relative to braincase breadth than *R. a. pestivulus* (Figure 5a). The nasal breadth females of *R. a. kalimantanensis* is generally larger relative to zygomatic breadth of *R. a. argentiventer* (Figure 5b)

Etymology

Named after the location on which the specimens were collected.

Pelage

Ventral fur with yellowish white tipping and base pastel gray to light gray; chest yellowish gray. Dorsum light brown on the tip and dark gray to purplish gray on the base, with sparse mixture of yellowish gray hairs. Forefeet grayish brown to yellowish brown, hindfeet grayish yellow to light blond.

Distribution

Widely distributed in Kalimantan (see Appendix for localities).

Rattus argentiventer saturnus Sody, 1941

Holotype

RMNH 9808 skin and skull collected by G. Stein

Type locality

Melolo, Sumba.

Diagnosis

Female *R. a. saturnus* from Sumba Island differ from *R. a. pestivulus* from Bali, Lombok, Sumbawa, Sangeang, Rinca, Komodo, Flores, Adonara, Timor, Alor, Tanimbar and Sulawesi in averaging slightly larger in nearly all skull characters except M²M², M³M³, IO, and IFB. Males differ from *R. a. pestivulus* in averaging slightly larger except for GSL, NL, NB, MSF, IFB, BL, BH, BB, PL, M¹W, CBL, BS, MSF, IFB, BL, and BH.

Males differ from *R. a. argentiventer*, in averaging slightly larger in all skull characters except LOD, RAP, M¹M¹, M²M², M³M³, ZB, HB, IO, and BOZP. Females differ from *R. a. argentiventer* by averaging slightly larger except for IFB.

Sody (1941) in describing *saturnus*, distinguished it only from *bali*, the taxon that applies to *R. argentiventer* from the Island of Bali. He noted that the differences between the two taxa were the length of tail relative to length of head and body and length of toothrows.

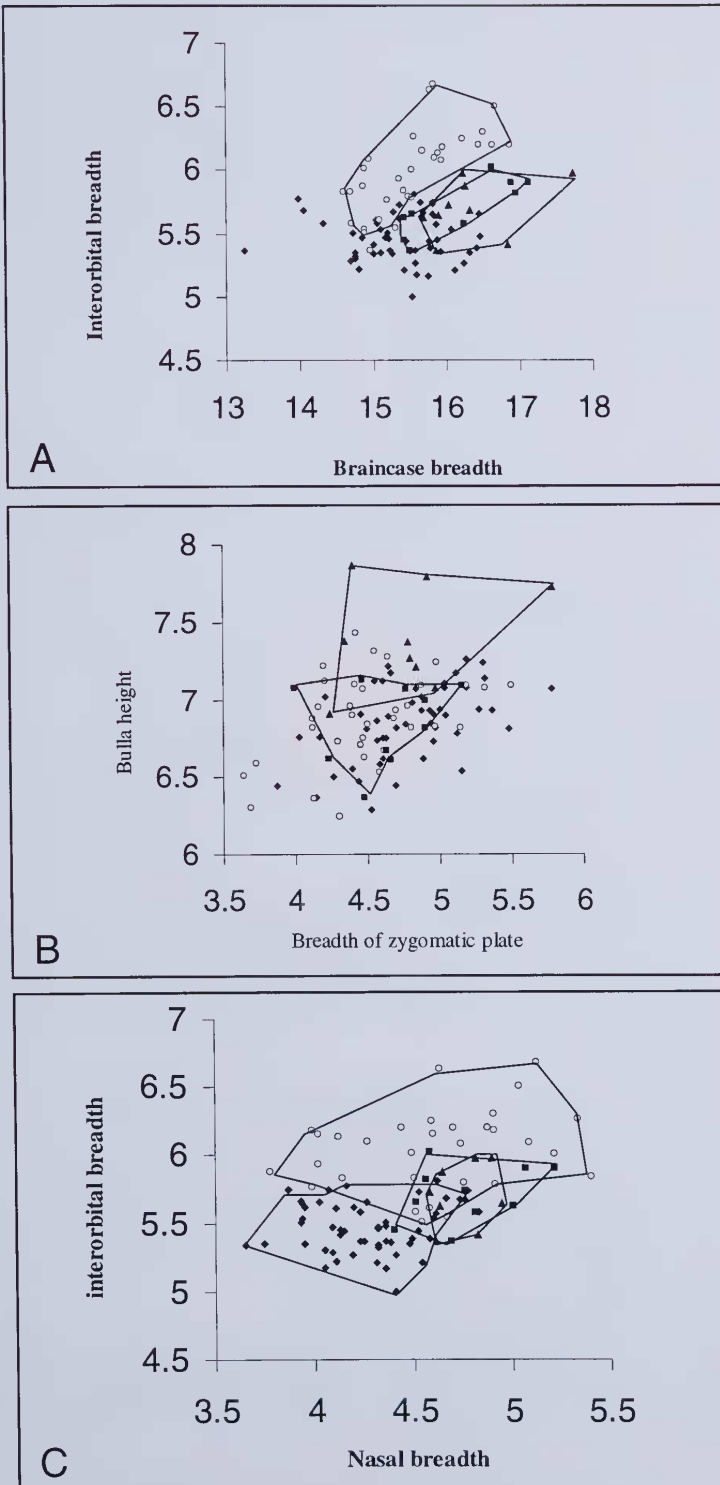


Figure 5 Bivariate plots of the female specimens. A. interorbital breadth against braincase breadth; B. Bulla height against breadth of zygomatic and C. interorbital breadth against nasal breadth. Groups of locality codes as for Figure 3.

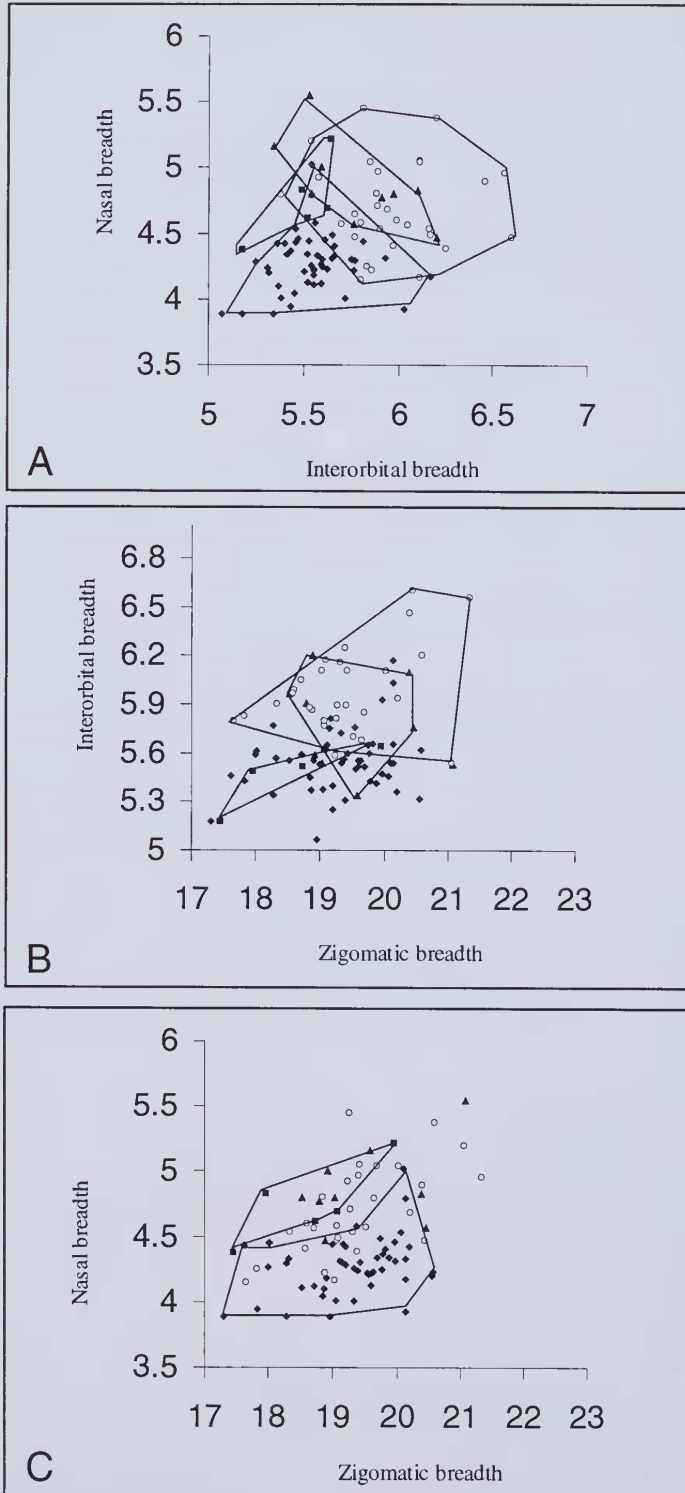


Figure 6 Bivariate plots of the male specimens. A. interorbital breadth against nasal breadth B. interorbital breadth against zygomatic breadth; C. Nasal breadth against zygomatic breadth. Locality group codes as for Figure 3.

Description

Musser (1972) described *R.a. saturnus* as having coarsely salt and peppered yellowish brown upper parts and silvery gray under parts as contrasted to the solid brown upper parts and creamy or buffy brown underparts of *R. rattus*. Juvenile and young adults have yellowish orange ear tufts that contrast conspicuously with the color of the head.

Distribution

Sumba Island

Rattus argentiventer pestivulus Thomas, 1921

Rattus rattus bali Kloss, 1921

Rattus argentiventer bali Kloss, 1921

Holotype

Adult female B.M. skin and skull in BMNH no. 21.2.9.11

Type locality

Laboehan Anak and Klungkung, Bali (Cotypes)

Diagnosis

Female *R. a. pestivulus* differ from female *R. a. argentiventer* by averaging slightly larger except for BOZP, IL, LB, and HF. The males differ by averaging slightly larger except for BOZP, MSF, BL, BH, PL, M²M², and M³M³.

Description

Thomas (1921) described *R. a. pestivulus* from the Sulawesi type specimen as fur thin and coarse, not definitely spinous. General color above dull reddish brown, sides rather gray, under surface sharply defined white, the hairs on the throat with gray bases. Hand and feet white. Tail of medium length thinly haired, light brown, almost white basally. The color variation with Bali specimens that are described by Kloss (1921) as dorsally grizzled ochraceous tawny and brownish black, below creamy white often with traces of a median grey stripe. Forefeet brown, hind feet white, broadly brown mesially. Skulls robust with rather short broad rostrum, broad palatal foramina and large bullae.

Distribution

Bali, Lombok, Sumbawa, Sangeang, Komodo, Flores, Adonara, Lembata, Alor, Timor, Tanimbar and Sulawesi

DISCUSSION

Although Chasen and Kloss (1928) believed specimens of the ricefield rat from Kalimantan to be

identical to typical *R. argentiventer* from Sumatra, the present analysis has shown that these populations are quite distinct on skull morphology. Differentiation on external characters is less pronounced with poor discrimination between these populations based on external measurements; typically less than 50% of individuals could be correctly classified. One external feature that does distinguish the population from the others is the more yellowish ventral surface due to an increased number of ventral hairs with yellow tips in Kalimantan specimens. This taxon is undescribed. At present it is best referred to as the "Kalimantan Population" of *R. argentiventer*. Musser (1973) argued that individuals from Sumba closely resemble those from Bali and allied these populations to those found further east on Lombok, Sumbawa, Komodo, Rinca, Flores and Timor. In the present analysis female specimens from Sumba are distinct from all other populations. In contrast, males from Sumba show overlap with other groups. I consider that *R. argentiventer* from Sumba are sufficiently distinct to warrant subspecies status as *R. a. saturnus* Sody, 1941.

Specimens from Sulawesi appear from this analysis to be referable to Bali, Lombok to Timor and the Tanimbar Islands group. Musser (1973) considered *R. argentiventer* to be recently introduced to Sulawesi and this is supported by my findings. Thomas (1921) described specimens from Sulawesi collected 1908 by Dr. Mohari from Manado as *Rattus pestivulus*. In the same year he redescribed *Rattus pestivulus*. Musser (1973; 1977) considered *R. pestivulus* to be a junior synonym of *R. argentiventer*. Also in 1921 Kloss described *R. r. bali*. Laurie and Hill (1954) considered that *R. r. bali* was a synonym of *R. argentiventer* as did Musser (1973). The specimens included in this study from Lombok were referred to *R. argentiventer bali* by Kitchener *et al.* (1990). Since my analysis indicates that the Sulawesi population is indistinguishable from those from Bali, Lombok, Sumbawa-Timor and Tanimbar Islands then two names become available for this taxon: *R. bali* and *R. pestivulus*. Thomas described *Rattus pestivulus* twice, once in May 1921 (Thomas 1921a) and once in an undated volume of *Treubia* in 1921 (Thomas 1921b). In the same volume of *Treubia*, but with a later pagination, Kloss described *R. bali*. The earlier page number for *R. pestivulus* gives it nomenclatural priority over *R. bali*, thus fixing the subspecific name for the *R. argentiventer* rats of Bali, Lombok, Sumba, Timor and the Tanimbar Islands as *R. a. pestivulus* (Thomas, 1921).

Specimens from Java, Sumatra and Thailand could not be separated in this study. This supports the view that *R. a. brevicaudatus* (Horst & de Raadt) from Java and *R. a. chaseni* (Sody) from Malaysia are identical with typical *R. argentiventer*.

The single specimen from Tanah Merah, Irian Jaya fitted within the scatter of *R. a. argentiventer* rather than with the geographically closer *R. a. pestivulus*. This is quite possible since the port at Tanah Merah has been used by navigators and trading vessels for centuries as a safe anchorage (Flannery 1990).

A major limitation to examining the morphological differences between populations of *R. argentiventer* is the marked variation related to individual age. In the present study it was necessary to separate juveniles and subadults from mature animals and to exclude the younger individuals from the analysis. Furthermore it was necessary to analyse males separately from females. For these reasons, it has proved impossible to provide concise diagnoses for the various morphologically distinct subspecies of *R. argentiventer* I have recognised on morphometric grounds. Kitchener and Suyanto (1996) discussed a similar pattern of morphological variation for a range of mammal groups in Indonesia. They concluded that the geomorphological and climatic diversity within the Indonesian Archipelago has provided an ideal setting for complex evolutionary processes leading to morphological change. They further suggested that many of these morphological changes might be of relatively recent origin. This observation is particularly pertinent in the case of taxa such as *R. argentiventer*, which may have expanded its geographic range in parallel with the spread of rice agriculture over the last few thousand years. An analysis of genetic markers will be needed to fully elucidate some of these recent evolutionary events.

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Appendix 1 List of locality, sex, number of specimens, latitude and longitude (ZRC = Zoological Reference Collection, Singapore; MZB = Museum Zoological Bogoriense, Bogor-Indonesia; WAM = Western Australian Museum, Perth Western Australia).

Malaysia and Thailand

Kualalumpur, Female, ZRC 2143, (3.08 N, 101.75 E)
 Pahang, Female, ZRC 87140, 87341 (3.37 N, 102.83 E)
 Perak, Female, ZRC 269/3, ZRC 3716, ZRC 4269, ZRC 4273, ZRC 6197 (4.87 N, 100.75 E)
 Perak, Male, ZRC 580/1, ZRC 584/1, ZRC 909/2, ZRC 2044, ZRC 4268 (4.87 N, 100.75 E)
 Bang-Penin-Siam, Female, ZRC 4274, ZRC 19073 (6.83 N, 101.25 E)
 P.Sirih-Siam, Male, ZRC 4227.

Sumatra

Jabung Lampung, Male, MZB11480 (5.48 S, 105.67 E)
 Kayu Agung, Female, MZB 12795 (3.40 S, 104.83 E)
 Kp. Halaban, Painan, Male, MZB 4864, MZB 4870, MZB 4873 (1.35 S, 100.57 E)
 Kp. Halaban, Painan, Female, MZB 4871 (1.35 S, 100.57 E)
 Loboek Sikaping, Female, MZB 4862, MZB 4865, (0.13 N, 100.17 E)
 Loeboek Sikaping, Male, MZB 4869, MZB 15345 (0.13 N, 100.17 E)
 Memudjan, Padang, Female, MZB 4866, MZB 4868, (0.95 S, 100.35 E)
 Padang, Male, MZB 15341, MZB 15347, MZB 15349 (0.95 S, 100.35 E).
 Padang, Female, MZB 4872 (0.95 S, 100.35 E)
 Mulyorejo, Way Abung, Female, MZB 13336, (4.83 S, 104.88 E)
 Mulyorejo, Way Abung, Male, MZB 13431 (4.83 S, 104.88 E)
 Pematangsiantar, Sumatra, Male, MZB 10459, MZB 10460 (2.95 N, 99.05 E)
 Sindang Datar Lebuay, Pulau Panggung, S. Lampung Female, MZB 11245 (2.80 S, 105.95 E)
 Wai Lima Lampung Male, MZB 337, MZB 361, (9.48 S, 104.52 E)

Java

Banyuwangi, Male, MZB 15348, (8.00 S, 114.08 E)
 Bagusan W.Java, Female, MZB 3379, MZB 3381 (6.32 S, 106.83 E)
 Bagusan W.Java, Male, MZB 3380, MZB 3382, MZB 3383, (6.32 S, 106.83 E)
 Bajulmati, Male, ZRC 8680 (7.93 S, 114.42 E)
 Bandung, Male, MZB 10211, (6.90 S, 107.60 E)
 Bogor Male, MZB 4880, MZB 4881, MZB 4886, MZB 4889, MZB 4898, MZB 7027, MZB 7028 (6.58 S, 106.78 E)
 Bogor Female, MZB 4887, MZB 4890, (6.58 S, 106.78 E)
 Boyolali, Female, MZB 10205, MZB 10207, MZB 10208 (7.53 S, 110.33 E)
 Boyolali, Male, MZB 10206, (7.53 S, 110.33 E)
 Cawang Jakarta, Male, MZB 3342, MZB 3392 (6.25 S, 106.87 E)
 Cawang Jakarta, Female, MZB 3439, MZB 8047, MZB 8054, MZB 8055 (6.25 S, 106.87 E)
 Jakarta, Female, MZB 180, (6.10 S, 106.88 E)
 Tj. Priok Jakarta, Male, MZB 3281 (6.10 S, 106.88 E)
 Cirebon, Female, MZB 2145, MZB 2146 (6.73 S, 108.57 E)
 Gandrungmangu, Cilacap, Male, MZB 13434 (7.53 S, 108.85 E)
 Garut W.Java, Female, MZB 4897, (7.22 S, 107.90 E)

Kresiek penameng W.Java, Female, MZB 12541 (6.10 S, 106.65 E)
 Kresiek penameng W.Java, Male, MZB 12542, (6.10 S, 106.65 E)
 Malang Female, MZB 4885 (7.98 S, 112.62 E)
 Palimanan Cirebon, Male, MZB 587 (6.73 S, 108.57 E)
 Palimanan Cirebon, Female, MZB 588 (6.73 S, 108.57 E)
 Pamanukan, Subang, Female, MZB 12361, MZB 12363, MZB 12367, MZB 12369, MZB 12561 (6.27 S, 107.82 E)
 Pamanukan, Subang, Male, MZB 12364, MZB 12365 (6.27 S, 107.82 E)
 Pandegglang, Female, MZB 4900, (6.30 S, 106.10 E)
 Randudongkal, Pemalang, Female, MZB 12375, MZB 12376, MZB 12564, MZB 12365 (7.10 S, 109.32 E)
 Randudongkal, Pemalang, Male, MZB 12377, MZB 12380, MZB 12383 MZB 12388, MZB 12389, MZB 12398, MZB 12563 (7.10 S, 109.32 E)
 Serang, N. Banten, Male, MZB 4892, MZB 4893, MZB 4894, (6.08 S, 106.08 E)
 Noesa Kambangan, Male, MZB 4903, MZB 5873 (7.75 S, 108.92 E)
 Noesa Kambangan, Female, MZB 4904, MZB 4905, MZB 4908, MZB 4909, MZB 8444 (7.75 S, 108.92 E).

Kalimantan

Barambai S. Kalimantan, Female, MZB 11114 (3.08 S, 114.64 E)
 Barambai S. Kalimantan, Male, MZB 11115 (3.08 S, 114.64 E)
 S. Kambat,Carbon-S. Kalimantan, Male, MZB 22418, MZB 22419, MZB 22424, MZB 22429 (3.06 S, 114.70 E)
 S. Kambat,Carbon-S. Kalimantan, Female, MZB 22420, MZB 22421, MZB 22422, MZB 22423, MZB 22425, MZB 22432, MZB 22433, MZB 22434 (3.06 S, 114.70 E)
 Singkawang, Female, MZB 4162 (0.90 N, 109.00 E)
 Tepian Batang (Pasir) Samarinda, Female, MZB 6390, MZB 6391 (0.50 S, 117.15 E).

Sulawesi

Loewoe (Kalonisatie Bone-Bone), Male, MZB 6412, MZB 6413 (2.50 S, 120.75 E)
 Makasar, Female, WAM 33095, (6.28 S, 119.87 E)
 Makasar, Male, WAM 33354, (6.28 S, 119.87 E)
 Makasar, Female, MZB 4876, MZB 4877, MZB 4879 (5.12 S, 119.40 E)
 Makasar, Sulawesi, Male, MZB 4878, MZB 2355 (5.12 S, 119.40 E)

Bali

Bali, Male, MZB 17229, MZB 17232, MZB 17236 (8.50 S, 115.27 E)
 Bali, Female, MZB 17231, MZB 17233, MZB 17234, (8.50 S, 115.27 E)
 Bali, Male, MZB 17237 (8.15 S, 114.43 E)
 Klungkung Male, MZB 197, MZB 201 (8.53 S, 115.40 E).

Lombok

Kuta Lombok, Female, MZB 17200 (8.92 S, 116.25 E)
 Swda Lombok, Male, MZB 4914 (8.75 S, 116.50 E)

Sumbawa

Desa Dahu, Male, MZB 17185, MZB 17186 (8.75 S, 118.43 E)

Desa Dahu, Female, MZB 17187, MZB 17188, MZB 17191 (8.75 S, 118.43 E)

Desa teluk Santong, Female, MZB 17182, (8.73 S, 117.89 E)

Dompoe, Soembawa., Female, MZB 4916, MZB 4917, MZB 4919, MZB 4921 (8.53 S, 118.47 E)

Sangeang

Desa Santong, Sangeang Is., Female, MZB 17184 (8.22 S, 119.01 E)

Desa Santong, Sangeang Is, Male, MZB 17183 (8.22 S, 119.01 E)

Dompoe, Soembawa, Male, MZB 4918, MZB 4920 (8.53 S, 118.47 E).

Sumba

Kananggar E. Sumba, Female, MZB 839 (10.05 S, 120.37 E)

Kambaniru, Female, MZB 4924, MZB 4939, MZB 4941, MZB 4942 (9.65 S, 120.32 E)

Melolo, Female, MZB 4931, (9.88 S, 120.67 E)

Sumba, Male, MZB 17165, MZB 17167, MZB 17168, MZB 17175 (9.63 S, 119.53 E)

Waikabubak, Male, MZB 17172, MZB 17177, (9.63 S, 119.53 E)

Waikabubak, Sumba, Female, MZB 17176, MZB 17178, MZB 17179 (9.63 S, 119.53 E)

Flores

Horowura Boru, Male, MZB 17195, (8.55 S, 123.65 E)

Kelimutu Woloaru, Female, MZB 17192, (8.70 S, 121.90 E)

Manggarai, Male, MZB 4923 (8.50 S, 120.25 E)

Maumere, Female, MZB 10492 (8.62 S, 122.23 E)

Mboera, Female, MZB 2396, MZB 2398 (8.57 S, 119.87 E)

Mboera, Male, MZB 2397, MZB 2399 (8.57 S, 119.87 E)

Wai Sano, Female, MZB 2401 (8.66 S, 120.51 E)

Wai Sano, Male, MZB 2402, MZB 2403 (8.66 S, 120.51 E)

Lembata

Belang Watokobu, Female, MZB 17193 (8.43 S, 123.37 E)

Adonara

Waiwerang, Horowura, MZB 17194 (8.33 S, 123.15 E)

Rinca

Rinca, Female, MZB 17196 (8.65 S, 119.67 E)

Tanimbar Is

Tanimbar, Male, WAM 43645, WAM 43653, WAM 43674, WAM 44390 (7.61 S, 131.46 E)

Tanimbar, Female, WAM 44317, WAM 43652 (7.61 S, 131.46 E)

Timor

Camplong Male, MZB 22413, MZB 22415, (10.03 S, 123.92 E)

Camplong Female, MZB 22414, MZB 22416 (10.03 S, 123.92 E)

Gunung Mutis, Timor, Male, MZB 17201 (9.55 S, 124.22 E)

Timor, Female, MZB 16747 (10.07 S, 123.88 E)

Alor

Alor, Male, MZB 17206, MZB 17207, MZB 17210, MZB 17214, MZB 17215 (8.25 S, 124.72 E)

Alor, Female, MZB 17208, MZB 17211, MZB 17212, MZB 17213, MZB 17219, MZB 17225, MZB 17226 (8.25 S, 124.72 E)

Komodo

Female, MZB 9001 (8.60 S, 119.50 E)

Male, MZB 9002 (8.60 S, 119.50 E)

Papua

Tanah Merah, Female, MZB 4875 (2.40 S, 140.35 E)